

THE MORPHOLOGY, LIFE-HISTORY, AND SYSTEMATIC
RELATIONS OF THE DIGENETIC TREMATODE,
UNISERIALIS BREVISERIALIS SP. NOV.,
(NOTOCOTYLIDAE), A PARASITE
OF THE BURSA FABRICIUS
OF BIRDS¹

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The genus *Uniserialis* was erected by Mary Beverley-Burton (1958) to contain *Uniserialis gippyensis*, a new species from the intestinal caeca and bursae Fabricii of mallard ducks, *Anas platyrhynchos platyrhynchos* Linn., taken near Ipswich, Suffolk, England. The generic diagnosis stated, "Notocotylidae Lühe, 1909; body flattened, small, rather pointed at the anterior end but rounded posteriorly; cuticula aspinose. Ventral surface with a single median longitudinal row of sessile glands. Oral sucker terminal, pharynx absent; esophagus short leading to intestinal bifurcation, ceca simple ending blindly near posterior extremity. Ventral sucker absent. Common genital pore ventral, median, anterior to intestinal bifurcation, near oral sucker. Two lobed testes, posterior and extracecal in position; external vesicula seminalis well developed. Cirrus sac elongate with internal vesicula seminalis; cirrus unarmed. Ovary median, between the testes, immediately posterior to Mehlis' gland; receptaculum absent. Uterus with ascending limb only, forming intracecal transverse slings. Metraterm long, with thickened walls and opening at the genital pore. Vitellaria follicular, in two lateral extracecal bands, running forward from anterior border of testes. Excretory pore dorsal and posterior, receiving the two main excretory vessels. Eggs numerous, small and operculate with long polar filaments. Adults in intestinal ceca and bursa Fabricius of birds. Genotype: *U. gippyensis* n. sp."

The genus was included in the subfamily Notocotylineae, family Notocotylidae, and distinguished from other genera: *Notocotylus* Diesing, 1839; *Catatropis* Odhner, 1905; *Paramonostomum* Lühe, 1909; *Quinquescrualis* Skvortzov, 1934; *Hofmonostomum* Harwood, 1939; and *Tristriata* Belopolskaia, 1953

MATERIAL AND METHODS

During the summer months of 1963, 1964, 1965 and 1966, over 5000 specimens of *Hydrobia salsa* were examined for infection by larval trematodes. The snails were identified by Dr. W. K. Emerson of the American Museum, New York. This is a somewhat rare, prosobranchiate species, described by Pilsbry (1905) as

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Paludestrina salsa. During the summers of 1963 and 1964, these snails were common in Nobska Pond near Woods Hole, Massachusetts, and most of the specimens were taken from an area near the connection of the pond with Vineyard Sound. In the fall of 1964, the pond was "treated" and most of the invertebrates, including snails, were killed. In the summer of 1965, *H. salsa* was found in nearby Oyster Pond and the study was continued. The results have been rewarding; ten different species of larval trematodes have been recognized; five of them are notocotylid cercariae. The methods and procedures employed have been described in earlier reports (Stunkard, 1960, 1966a, 1966b, 1967) on the morphology and life-cycles of notocotylid species. In the (1966a) paper, the writer reported that the five notocotylid cercariae included representatives of all three larval types dis-

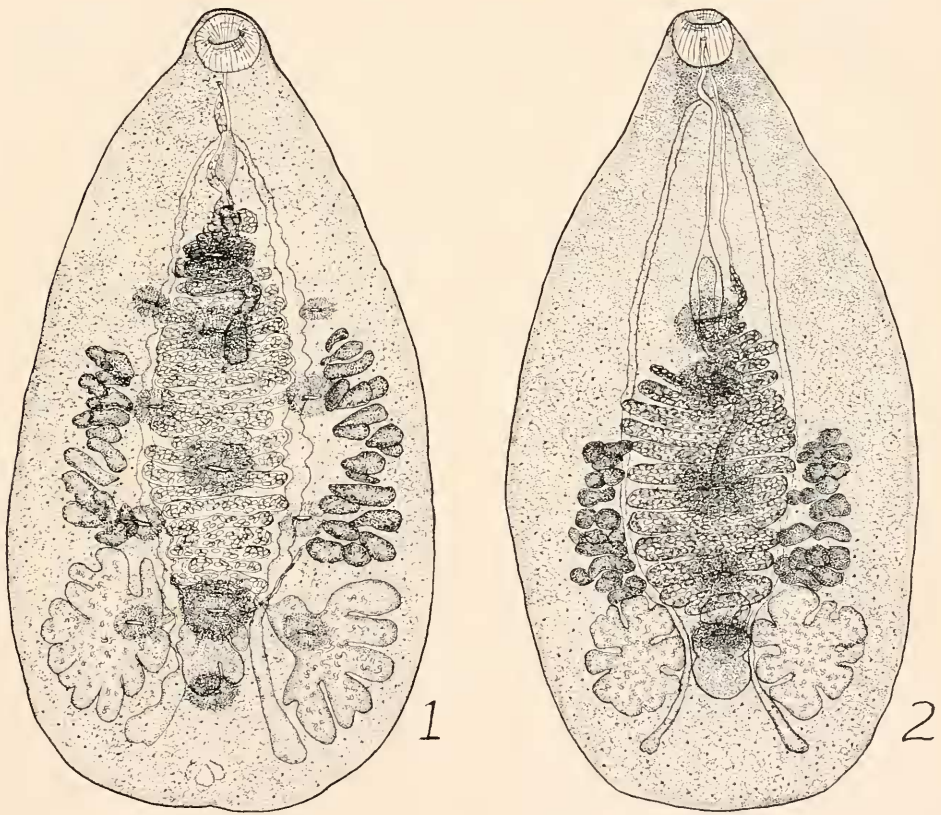


Plate I

FIGURE 1. *Uniserialis breviserialis*, adult specimen, ventral view, somewhat flattened, fixed and stained, 2.3 mm. long, from the bursa of a domestic duckling, 12 days after metacercaria was fed.

FIGURE 2. *Uniserialis gippensis* Beverley-Burton, 1958, paratype specimen, ventral view, 1.62 mm. long, from bursa of *Anas platyrhynchos*. The ventral glands are not visible in this specimen; their size and location on other worms were determined and added in the drawing.

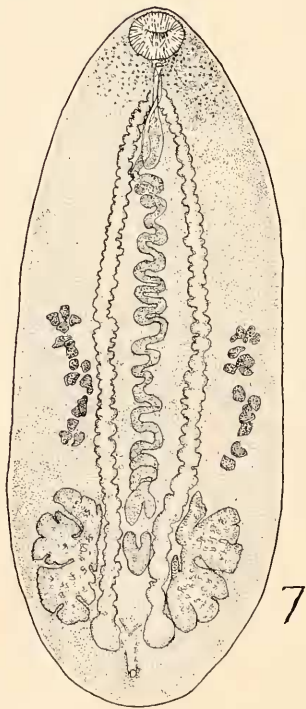
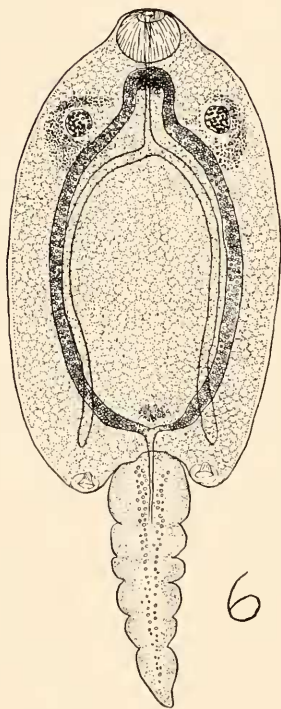
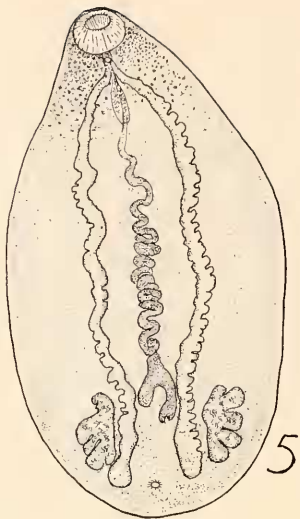


Plate II

tinguished by Rothschild (1938) on differences in the structure of the excretory system and designated as the *Yenchingensis*, the *Monostomi*, and the *Imbricata* Groups. Two of the cercariae belong to the *Yenchingensis* Group; they develop to maturity in the digestive caeca of ducklings and were described by Stunkard (1966b) as *Nototylus minutus* Stunkard and Dunihue, 1931 and *Notocotylus atlanticus* sp. nov. Two cercariae belong to the *Monostomi* Group; they develop in the lumen of the intestine of chicks and ducklings and were described by Stunkard (1967) as *Paramonostomum alveatum* (Mehlis in Creplin, 1846) and *Paramonostomum parvum* Stunkard and Dunihue, 1931. The fifth cercarial species belongs to the *Imbricata* Group; these larvae develop in the bursa Fabricius of chicks and ducklings, and form the subject of the present report.

These worms are similar in many respects to those from the intestinal caeca and bursae Fabricii of mallard ducks, described by Beverley-Burton (1958) as *Uniserialis gipphyensis*; compare Figures 1 and 2. According to Beverley-Burton, the worms described as *U. gipphyensis* have only one row of ventral glands, median in position and five in number. The present specimens have the five median glands and, in addition, four small lateral glands on either side, situated in the intervals between the median glands. These small lateral glands are recognizable in most living specimens but are rarely visible in fixed and stained preparations. Indeed, the large, median glands can not be seen in many whole-mount individuals. It appeared possible that the present worms are congeneric with those described by Beverley-Burton and in an attempt to resolve the problem, the specimens of *U. gipphyensis* deposited in the British Museum (Natural History) were borrowed through the kindness of Mr. Stephen Prudhoe. The material in the British Museum consists of one slide on which there are three specimens, all lightly stained. The largest and apparently the most representative specimen, ringed on the coverglass, is reproduced (Fig. 2); it is 1.62 mm. long; 0.81 mm. wide; oral sucker, 0.14 mm. in diameter; distance from anterior end to base of cirrus sac, 0.66 mm.; testes measure 0.25 by 0.19 mm.; ovary, 0.13 mm. in diameter; vitellaria extend 0.32 mm. and are situated in the posterior half of the body. In this specimen the median glands are not recognizable although they can be seen on the other two worms. The other worms are slightly smaller but very similar, and all agree completely with the specific description as given by Beverley-Burton. No lateral glands are visible on any of the specimens, but the staining is faint and it is probable that if present, they would not be recognizable.

The *Imbricata* cercariae are the largest of the notocotylid larvae found in *H. salsa*. They emerge principally after 11 AM and some were swimming at 4 PM, but most of them encysted after swimming for an hour or two. Feeding of encysted metacercariae to chicks and domestic Pekin ducklings yielded developing and

FIGURE 3. *U. breviserialis*, redia, natural infection, fixed under a coverglass, 0.87 mm. long.

FIGURE 4. *U. breviserialis*, juvenile specimen, flattened under a coverglass, stained and mounted, 0.75 mm. long, four days in domestic duckling.

FIGURE 5. *U. breviserialis*, juvenile specimen, flattened under a coverglass, stained and mounted, 1.12 mm. long, six days in a domestic duckling.

FIGURE 6. *U. breviserialis*, young cercaria, from fixed and stained specimen, flattened under a coverglass, with details added from sketches of living specimens.

FIGURE 7. *U. breviserialis*, juvenile specimen, flattened under a coverglass, stained and mounted, 1.56 mm. long, nine days in a domestic duckling.

gravid worms, all of which were taken from the bursa Fabricius. The worms adhere tenaciously to the wall of the bursa and when removed, the caeca are bright red with blood from the host. The corpuscles are clearly visible in fixed and stained worms. Both median and lateral ventral glands are visible in juvenile worms, six days in a chick, as well as in sexually mature specimens. A series of drawings (Figs. 4, 5 and 7) shows development of worms from four to nine days in the bursa of domestic ducklings. The smallest sexually mature worm, fixed without pressure, is 1.19 mm. long and 0.65 mm. wide; the vitellaria extend through a distance of 0.24 mm.; the testes measure 0.18 by 0.16 mm.; the cirrus sac is 0.19 mm. long and 0.055 mm. wide; the ovary is 0.16 mm. long and 0.072 mm. wide; Mehlis' gland is 0.080 mm. wide and 0.060 mm. long. The metacercariae were fed August 14, 1965, and the bird was autopsied August 30, 1965.

DESCRIPTIONS

Adult (Fig. 1)

The body is ovate, much flattened, more pointed anteriorly and rounded posteriorly. It is convex dorsally, concave ventrally, with the edges of the body turned ventrad and mediad. Fixed and stained specimens measure 1.19 to 2.54 mm. in length and 0.56 to 1.66 mm. in width. The cuticula is thin; fine spines were observed on the ventral surface of living worms but they do not show on fixed and stained specimens. The body wall is delicate, the musculature is weak; the longitudinal muscles are best developed. The ventral surface bears five median, protrusible glands that are conspicuous in living specimens. They are circular to oval in outline with transverse slit-like openings. The anterior and posterior glands measure 0.12 to 0.15 mm. in diameter; the three middle ones are somewhat larger and measure 0.16 to 0.20 mm. in diameter. The most anterior gland is situated about its diameter posterior to the base of the cirrus sac; the second gland is at the level of the anterior ends of the vitellaria; the third gland is near the middle of the vitelline zone; the fourth gland is at or slightly posterior to the level of the caudal ends of the vitellaria; and the most posterior gland is at the ovarian level. The lateral glands are smaller than the median ones; they measure 0.09 to 0.12 mm. in diameter, and are situated in the intervals between the median ones. The three anterior ones are in the fields of the digestive caeca and the most posterior glands are ventral to the antero-median lobes of the testes.

The excretory pore is dorsal, about midway between the ovary and the posterior end of the body. The bladder is small and the collecting ducts extend forward, forming a loop that crosses the body anterior to the cerebral ganglia. Dendritic branches from the longitudinal ducts form a complex network of excretory channels.

The oral sucker is terminal, 0.13 to 0.20 mm. in diameter; the mouth is slightly ventral; the esophagus is short, about the length of the sucker; the caeca extend posteriad, lateral to the uterine loops, turn mediad to pass between the testes and ovary, and end blindly posterior to the testes.

The testes are situated in the extracaecal areas near the posterior end of the body. They are deeply lobed, and vary in size from 0.18 by 0.16 mm. to 0.50 by 0.375 mm. Sperm ducts arise at the antero-median faces and unite a short distance anterior to Mehlis' gland to form the vas deferens which passes anteriad, dorsal to

the uterus. At about the level of the anterior ends of the vitellaria, it expands to form a coiled external seminal vesicle which continues the forward course to the cirrus sac. A coiled internal seminal vesicle occupies the posterior third to one-half of the cirrus sac and is continued by the ejaculatory duct; both are enclosed in prostatic cells. The cirrus sac leads to the genital pore, located anterior to the cerebral ganglia and at or near the level of the posterior border of the oral sucker. The cirrus sac is dorsal to the metraterm and measures from 0.19 to 0.40 mm. in length and 0.055 to 0.15 mm. in greatest width. It is located in the anterior fourth of the body.

The ovary is lobed, usually longer in the antero-posterior axis and increases in size as the worm matures. In a young specimen it may be 0.16 by 0.072 mm. and in a large, fully mature worm it may be 0.28 by 0.20 mm. The oviduct arises at the antero-dorsal margin and receives a common vitelline duct as it enters Mehlis' gland, which is somewhat smaller and immediately anterior to the ovary. There is no seminal receptacle and the initial coils of the uterus are filled with spermatozoa. The uterus passes forward in intercaecal, transverse loops, 15 to 25 in number, to communicate with the metraterm. The metraterm is somewhat shorter than the cirrus sac, is ventral in position, has a weak muscular wall, and opens at the genital pore posterior to the opening of the cirrus sac. The vitellaria consist of 15-20 discrete, irregularly shaped follicles which occupy the extracaecal areas from the testes to the level of the external seminal vesicle. They extend through a distance of 0.22 to 0.62 mm. and in large part are situated in the middle third of the body. Collecting ducts course posteriad along their median faces and at the posterior end of the vitellaria pass mediad, ventral to the caeca, then turn dorsad, joining above Mehlis' gland to form a vitelline receptacle from which the short common duct leads to the oviduct. The eggs are operculate, 0.019 to 0.020 mm. long, 0.011 to 0.013 mm. wide, provided with long polar filaments, and embryonated when passed.

Redia (Fig. 3)

The rediae are oval to sausage-shaped to elongate; extended, they are cylindrical with conical posterior ends. Small rediae are colorless, actively motile but without feet, and one which measured 0.10 mm. in length contained a small daughter as well as germ balls of developing cercariae. Locomotion is accomplished by contraction of the circular and longitudinal muscles of the body wall. As the rediae grow and become filled with progeny, movement is less and less active. Older rediae have orange-yellow droplets, 0.002 to 0.006 mm. in diameter, in the body wall; the largest extend to a length of 1.00 mm.; the specimen shown in Figure 3, fixed and stained, is 0.87 mm. long and 0.23 mm. wide. In the older rediae the pharynx measures 0.042 to 0.052 mm. in diameter, the esophagus is about the same length, and the intestine, which extends to the middle of the body in young rediae, is restricted to the anterior third or fourth of the body length. The birth pore is ventral at the level of the esophagus. There are two excretory pores, one on either side near the middle of the posterior half of the body. From each pore a duct passes forward, just past the middle of the body where it divides into anterior and posterior branches. Each branch terminates in a flame-cell, one at the level of the esophagus, the other posterior to the excretory pore.

Cercaria (Fig. 6)

The cercariae are large; they emerge from the rediae in very immature condition, about one-half the size they eventually attain. On emergence from the redia into the haemal sinus of the snail, the tail is so small and weak that the cercaria cannot swim if liberated by crushing the snail. Figure 3 is made from sketches of a young specimen. Alive, it extended to a length of 0.30 mm., fixed and stained it is 0.20 mm. long and 0.12 mm. wide. In it the excretory ring is complete but the common stem extends into the tail and the excretory pores are situated on the sides of the tail. The excretory system develops in the manner described for Imbricata cercariae by Rothschild (1938: Figs. 30, 31, 32, 34, 38), with the primary collecting ducts fusing anteriorly to form the loop that extends across the body anterior to the cerebral ganglia and the median eye-spot. As the cercaria matures in the haemal sinuses of the snail, the ring becomes filled with the concretions 0.003–0.005 mm. in diameter and the portion of the excretory system in the tail atrophies as a new definitive excretory pore develops from the dorsal wall of the expanding excretory bladder. The study of the flame-cell pattern has been disappointing. It is probable that the formula is $2 [(3+3+3)+(3+3+3)]$, as reported by Martin (1956) and Odening (1966) for other notocotyloid cercariae. In young cercariae the formula is $2 [(1+1+1)+(1+1+1)]$, and in older cercariae the anterior and posterior groups each have three cells, but the cystogenous cells fill so early that not all the flame-cells and capillaries have been observed in the mid-region of the body. As noted, the cystogenous cells fill the parenchyma and obscure other structures; the secretion appears in the form of short, bacilliform rods. Normally emerged cercariae vary from 0.30 to 0.60 mm. in length and 0.14 to 0.25 mm. in width. The postero-lateral ends of the body bear eversible, retractile locomotor appendages which function in creeping movements of the body. When the body is extended, they are close together, separated only by the base of the tail which is between and ventral to them; as the body contracts they separate and serve as fulcrum for the next extension of the body. The tail is simple, slender, 0.04 to 0.08 mm. in width at the base, and about the same length as the body. When either is contracted, the other is elongated. The wall of the tail is composed of external circular and internal longitudinal muscles which enclose loose parenchymal tissue. In swimming, the body is contracted, bent ventrally, almost circular, while the tail is extended and lashes vigorously. The ocelli are formed while the cercariae are in the rediae (Fig. 3), and increase to a diameter of 0.016 to 0.024 mm.; they are provided with lenses and are connected by short nerves to the cerebral ganglia. The median eye-spot, usually lacking in young cercariae, often becomes well organized as a dark ring in emerged individuals. Diffuse, dendritic strands of pigment surround the ocelli, permeate the anterior end of the body and extend posteriorly, especially along the digestive caeca. The oral sucker measures 0.04 to 0.05 mm. in diameter, the esophagus is about the same length; it passes backward below the commissure of the nervous system and above the excretory ring. Immediately behind the level of the cerebral ganglia it communicates with the intestinal caeca. The caeca extend posteriad, dorsal and medial to the excretory ring, which they cross near the posterior end of the body to terminate in the extracaecal areas. Deeply staining germinal cells, situated immediately anterior to the caudal end of

the excretory ring, are the primordia of the gonads, and a strand of these cells extends anteriorly in the median plane.

Metacercaria

Infected snails were identified by isolation. The cercariae begin to emerge about 11:00 AM and swim toward the light side of the container. By 3:00 PM, almost all are encysted, on the shell of the snail from which they emerged, the wall of the container, or on strands of algae. The cysts are the largest of the five notocotylid species and average measurements are 0.195 mm. in external and 0.175 mm. internal diameter. The worms do not develop in their cysts; they are infective immediately and become sexually mature in about two weeks in the bursae Fabricii of ducklings and chicks.

DISCUSSION

The present specimens are very similar, morphologically, to *Uniserialis gippyensis* Beverley-Burton, 1958. They are from the same site, the bursa Fabricius of birds, and from the same or related host species. The principal difference is the presence on the ventral surface of lateral glands which were not described for *U. gippyensis*. But these glands are rarely visible in fixed and stained specimens. If they do occur in *U. gippyensis*, the present specimens are obviously congeneric with those of Beverley-Burton, and on that presumption, they are described as a new species, *Uniserialis breviserialis*. Type and paratype specimens are deposited in the Helminthological Collection of the U. S. National Museum under the numbers 61,186 and 61,187. Specific differences between *U. gippyensis* and *U. breviserialis* are recognizable in the length of the cirrus sac and the location of the gonads and vitellaria. In *U. gippyensis* the cirrus sac is about twice as long; it extends one-third of the length of the body; in *U. breviserialis* it is short, less than one-fourth of the body length. In *U. gippyensis* the reproductive organs are more posteriorly situated; the vitellaria are in the posterior half of the body whereas in *U. breviserialis* the vitellaria are situated largely in the middle third of the body.

The validity of the genus *Uniserialis* is questionable. Baer and Joyeux (1961) suppressed *Uniserialis* as identical with *Notocotylus* Diesing, 1839 and the presence of lateral glands on the ventral surface of the present specimens seemingly supports that action. But there are other considerations which may validate the genus *Uniserialis*. Miriam Rothschild (1938) recognized three types of notocotylid cercariae, designated the Yenchingensis, the Monostomi, and the Imbricata Groups, respectively, based on the structure of the excretory system. Stunkard (1966a) found that *Notocotylus minutus* and *Notocotylus atlanticus* have Yenchingensis-type cercariae and develop in the intestinal caeca; that *Paramonostomum alveatum* and *Paramonostomum parvum* have Monostomi-type cercariae and develop in the lumen of the intestine; whereas the present species, *Uniserialis breviserialis*, has Imbricata-type cercariae and localizes in the bursa Fabricius. The apparent correlation of cercarial type, generic allocation and sites of infection is disturbed by the report of Rothschild (1941) that two species of Yenchingensis-type cercariae developed in the intestinal caeca of ducks into flukes of the genus *Paramonostomum*. Furthermore, Odening (1966) reported that five species of *Notocotylus*: *N. pacifer* (Noble, 1933); *N. ephemera* (Nitzsch, 1807); *N. noyeri* Joyeux, 1922; *N. regis*

Harwood, 1939; and *N. ralli* Baylis, 1936, have Monostomi-type cercariae, whereas *Catatropis verrucosa* (Fröhlich, 1789) has Imbricata-type cercariae.

Odening stated that the cercariae of *C. verrucosa* lack eye-spots, have short, stumpy tails, and encyst in the snails in which they are produced, viz., *Segmentina nitida* (O.F.M.) and *Gryaulus albus* (O.F.M.). The adults were raised in ducklings. The life-cycle of *C. verrucosa* as given by Odening recalls the account of Joyeux (1922) who reported that stumpy-tailed cercariae without eye-spots from *Planorbis rotundatus* Poiret developed in ducklings to adults which were identified as *Notocotylus attenuatus*. The adults were not described but Dubois (1951) examined specimens deposited in the Zoological Institute of the University of Neuchâtel and declared that the worms were not *N. attenuatus* but *C. verrucosa*. Szidat (1930) had reported that *Cercaria cphemera* Nitzsch, 1807 from *Planorbis cornucis* is the larva of *C. verrucosa*, but L. and U. Szidat (1933) assigned the adults to a new species, *Notocotylus thienemanni*. Erkina (in Skrjabin *et al.*, 1963) described a large cercaria from *Bithynia tentaculata* and *Bithynia leachi* with three eye-spots and a long tail as the larva of *Catatropis verrucosa*. Martin (1956) described *Catatropis johnstoni* n. sp., and its life-cycle. The larvae were found in the prosobranch snail, *Cerithidea californica*; they had long tails, eye-spots, and belonged to the Imbricata-group of cercariae.

Discussing the reports of Erkina and Martin, Odening (1966: 229) stated, "Es scheint kaum möglich, dass ein und dieselbe Art zwei ganz verschiedene Larventypen hat; folglich kann es sich wohl nur bei einem der beiden Zyklen um den von *C. verrucosa* handeln. Ob es sich nun hierbei um zwei Arten handelt, die als Adulti kaum oder nicht unterscheidbar sind, kann vorerst nicht entschieden werden. . . . Es erhebt sich die Frage, ob nicht jener merkwürdige, von Joyeux entdeckte Typ monostomer Cercarien für die Gattung *Catatropis* charakteristisch wäre. Diese Frage lässt sich in Anbetracht der Differenz zwischen den Angaben von Erkina und den hier geschilderten Ergebnissen (sowie denen von Joyeux) über *Catatropis verrucosa* nicht beantworten. Leider liegen keine Angaben über Entwicklung anderer *Catatropis*-Arten vor, bis auf die Resultate von Martin (1956) über '*Catatropis johnstoni* Martin, 1956.' Die Zugehörigkeit dieser Art zur Gattung *Catatropis* ist jedoch fraglich, denn es heisst in der Diagnose: 'Median ventral glandular ridge from ovarian to mid-cirrus level. Lateral ventral glands lacking.'

"Diese Art würde in dem gleichen Verhältnis zur Gattung *Catatropis* stehen wie die Gattung *Uniserialis* Beverley-Burton, 1958, zur Gattung *Notocotylus*. Andererseits ist der von Martin beschriebene mediane Drüsenkiel aus einzelnen querovalen Drüsen zusammengesetzt. Die Cercarie von '*Catatropis johnstoni*' gehört zur 'Imbricata'-Gruppe (Rothschild), hat einen langen Schwanz und drei Augen. Die zugehörigen Redien schmarotzen bei einem Prosobranchier, der an der californischen Küste lebt. Die Gruppenzugehörigkeit der von Erkina für *C. verrucosa* beschriebenen Cercarie ist nicht eindeutig erkennbar; aus den Zeichnungen könnte man vielleicht entnehmen, dass es sich um eine Cercarie der 'Yenchingensis'-Gruppe handelt (vgl. auch Ševcov und Zaskind, 1960). Der von Joyeux entdeckte stummelschwanzige und augenlos Type monostomer Cercarien wurde auch bei *Parapronocephalum symmetricum* Belopol'skaja, 1952, nachgewiesen (s. Skrjabin *et al.*, 1955). Die Redien schmarotzen in Meeresprosobranchiern. Die Cercarie gehört zur 'Monostomi'-oder zur 'Imbricata'-Gruppe (die Gruppen-

zugehörigkeit wurde nicht angegeben, es kann nur die 'Yenchingensis'-Gruppe ausgeschlossen werden)."

Uniserialis breviserialis, like species of *Catatropis*, has Imbricata-type cercariae. The significance of groups of notocotyloid cercariae, their generic allocations and infective sites are yet dubious, and it is apparent that discrimination and discretion will be required for a solution of the taxonomic problems in the family Notocotyliidae.

SUMMARY

Imbricata-type cercariae from *Hydrobia salsa*, a brackish-water, prosobranch snail taken near Woods Hole, Massachusetts, emerge shortly before noon, are photopositive and encyst after swimming for a few minutes to three to four hours. Metacercariae were fed to chicks and domestic ducklings and developed to mature worms after about two weeks in the bursae Fabricii of these birds. Adult and larval stages are described and figured. The worms belong in the family Notocotyliidae and are assigned to the genus, *Uniserialis* Beverley-Burton, 1958. Systematic problems of genera in the family are discussed.

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